

BRACHIOPOD FOOD AND FEEDING PROCESSES

by H. M. STEELE-PETROVIĆ

ABSTRACT. By considering the available relevant data on morphology, physiology, histology, and biochemistry of the lophophore and digestive tract of brachiopods, and by filling in gaps in the knowledge with analogies drawn from filter-feeding bivalves, a relatively detailed account of feeding processes in brachiopods is presented. It is shown that, except in the expulsion of wastes, similar feeding processes appear to occur in both the inarticulates and articulates. The articulate method of expelling faeces through the mouth has little disadvantage over the inarticulate method of expulsion through the anus. Direct evidence shows that brachiopods are able to assimilate dissolved substances; indirect evidence suggests that bacteria and colloids are utilized, that organic detritus and some algae are important food sources, and that animal forms of life are not important foods for brachiopods. There is no reason to suggest that the food categories of fossil brachiopods differed from those of extant forms. Suggestions are made on how to obtain more information on the food and feeding processes in brachiopods.

THE structure of fossil communities cannot be understood without knowing how the animals that lived together in these communities interacted. One of the major regions of potential interaction is competition for food. Since brachiopods were a dominant element in Palaeozoic communities of Ordovician age and younger, knowledge of the food and feeding methods of brachiopods is necessary to understand trophic relationships in the early invertebrate communities, and changes in these relationships with time. Although there is no direct evidence on the food of brachiopods in the past, they are a conservative group of animals, and one would expect the food and feeding processes of Recent species to be similar to those of fossil forms. The food of articulate brachiopods has been a subject of interest in recent palaeontological literature; information has been presented based on examination of gut contents (McCammon 1969; Levinton and Suchanek 1972; Suchanek and Levinton 1974) and on evidence for uptake of dissolved substances (McCammon 1969; McCammon and Reynolds 1972). However, these approaches do not treat all aspects of brachiopod food, and therefore do not lead to a comprehensive interpretation of what the animals in general feed on.

To obtain a broader knowledge of brachiopod food it is necessary to understand how particles are trapped, ingested, and digested, and how waste material is expelled; thus it is essential to have information on morphology, histology, physiology, and biochemistry of the trapping and digestive organs. Sufficient relevant information has been published on these aspects of the biology of brachiopods to enable much reconstruction of the feeding processes, although major gaps in the knowledge remain. However, there are certain similarities between digestive tracts of brachiopods and those of filter-feeding bivalves; and digestion in bivalves is much better understood than that in brachiopods. Therefore information from bivalves on processes that appear to have analogues in brachiopods can be used to fill some gaps in the brachiopod reconstruction. Similarities between inarticulates, articulates,

and bivalves have been used to set up a general model here for feeding processes in brachiopods. After this model was formulated, Professor Gareth Owen kindly sent me his unpublished information on the digestive tracts of the articulate *Tegulorhynchia* and *Terebratella*, which provides the first evidence on the functioning of the digestive diverticula in brachiopods. That these data demonstrate the essential similarity between the action of the digestive diverticula in brachiopods and in bivalves is a confirmation of an essential aspect of my model; this increases the probability that interpretations of other aspects of brachiopod feeding based on comparisons with bivalves are also valid.

FUNCTIONS OF THE TRAPPING ORGANS

The lophophore, the trapping organ of brachiopods, consists of two arms (brachidia) looped symmetrically one on each side of the mouth. Each brachidium consists of a cartilaginous brachial axis that bears along its entire length both a ciliated food-groove bounded by a muscular lip, and two parallel rows of long, slender flexible filaments perpendicular to the axis. Cilia occur around the brachial axis, on the sides and fronts of the filaments, and on the backs of inarticulate filaments; but they are usually rare or absent on the backs of articulate filaments (see Chuang (1956) and Rudwick (1970, pp. 117ff.) for descriptions of brachiopod lophophores). The structure of the lophophore is similar in all extant families of brachiopods, and fossil evidence shows that it has not changed, at least in one group of terebratulids, since the Cretaceous (Rudwick 1970, p. 120). Since the preservable parts of the different brachiopod orders have remained similar throughout the evolution of these groups, it is assumed that the basic structure of the lophophore and alimentary tract has not changed, and that brachiopods have always fed in the same manner.

When a brachiopod is feeding, the lateral cilia on the filaments beat in a metachronal wave from the frontal to abfrontal surface of the filaments, and produce an inhalant water current that passes between the filaments from the frontal to abfrontal side (Atkins 1958, 1960). Some of the material that is suspended in the incoming water is collected by the lophophore, but a large proportion is carried through it and out with the exhalant current (Rudwick 1962; Steele-Petrović 1975). Bullivant (1968) has suggested that sharp deflection of the water around the tentacles causes certain suspended particles to be thrown against the frontal surfaces of the tentacles, and that selection of these particles depends on their velocity, density and size, radius of curvature of the deflection, and viscosity of the sea-water. He introduced the term 'impingement-feeders' for animals that collect potential food material in this manner. Once particles have impinged on the frontal surfaces of brachiopod filaments, no sorting appears to take place (Rudwick 1970, p. 121). The material is carried indiscriminately to the base of the filaments in a local current created by the frontal cilia (Chuang 1956), and then into the ciliated food-groove which leads directly to the mouth. As Chuang noted for *Lingula*, other suspended particles may contact the outer surface of the brachial lip; the beating of cilia that occur there subsequently carries this material over the lip and into the food-groove.

It is generally assumed that brachiopods continuously feed when the valves are open and an inhalant current is being produced. However, trapping and ingestion

of particles probably ceases when the stomach becomes full; for (as is discussed later) ingested particles, regardless of food value, all appear to be retained in the stomach while digestion takes place. A brachiopod can prevent particles from reaching the mouth by stopping the frontal cilia and closing the food-groove; this should not prevent lateral cilia from maintaining an inhalant current for continued oxygen supply. Trapping and ingestion probably resume after digestion of food and expulsion of undigested material from the stomach have occurred. If the feeding system becomes overloaded with trapped material, the only recourse is wholesale rejection as described by Chuang (1956), Atkins (1958, 1960), and Rudwick (1962, 1970). The animal ceases feeding by closing the lip of the food-groove and by stopping the beat of the lateral cilia; mucus secreted by the filaments engulfs the particles and the frontal cilia reverse direction of beat, or in the case of *Lingula*, where adjacent rows of frontal cilia appear to beat permanently in opposite directions (Chuang 1956), those beating towards the tips of the filaments beat more strongly. The mucus-bound particles are thus carried to the tips of the filaments and on to the mantle surface from where they are rejected as pseudofaeces. In some brachiopods reversal of the lateral cilia aids in the rejection process by producing a current that flows in the opposite direction to the feeding current. Chuang (1956) has shown that *Lingula* can get rid of single large particles while continuing to feed. Only Atkins (1958) has observed a simultaneous acceptance of some particles and rejection of others by the lophophore, and she stated that this action was seen only in a few specimens, although in several different species. She observed that occasionally those particles that were trapped by the frontal filaments were transported to the tips of the filaments and rejected from the shell, while those trapped by the abfrontal filaments were transported in the opposite direction to the food-groove. There is no information on the details of water-flow around the filaments, and on whether particles hitting the two sets of filaments differ. However, it seems unlikely that the action described by Atkins is used as a sorting mechanism, as she suggested, for it appears to occur too rarely.

The role played by mucus in the transportation of accepted particles along the filaments to the food-groove is probably minor; Orton (1914) claimed that a mucus sheet aids in the capture and retention of food particles, and that these particles when bound in mucus are easily transported along the filaments (he insinuated towards the mouth) by frontal cilia. However, Chuang (1956) observed that particles are water-borne on the frontal surfaces of the filaments of *Lingula*, and that mucus is unimportant except under unfavourable conditions such as abnormally high turbidity. Rudwick (1962) saw that mucus was produced only when a rejection mechanism was working, and then a sheet of mucus entangled the unwanted particles. R. G. B. Reid has suggested to me that minute, indiscernible amounts of mucus may impart a stickiness to particles that may be important. However, one can conclude that Orton was describing a rejection mechanism. He did not mention what his animals were fed, but Rudwick (1962) found that rejection took place when brachiopods were fed even dilute suspensions of carmine, graphite, carborundum, starch, or milk; materials that are usually used in the study of ciliary currents of suspension-feeding animals. By contrast with transport along the filaments, potential food particles that contact the outer surface of the brachial lip may or may

not be entangled in discernible amounts of mucus before they are carried into the food-groove (Chuang 1956); but all particles, once they have reached the ciliated food-groove, are bound into a string of mucus for transport to the mouth (Richards 1952; Chuang 1956).

Thus it seems that brachiopods are non-selective feeders, and either accept or reject all material that is collected from the inhalant current. Because of their open filamental structure they are able to trap only a small proportion of particles that are suspended in the incoming water. Most of these particles are probably non-motile. As suggested by Bullivant (1968), rapidly moving protists can probably readily escape from the exposed frontal edges of the filaments. If mucus were present it would aid in holding the motile forms, but not much mucus is secreted by the filaments during the normal feeding process. However, mucus is secreted normally by the outer surface of the brachial lip and by the ciliated food-groove; and swimming protists that make direct contact with these areas would become entangled in mucus and trapped. The muscular lip probably also aids in retaining any motile forms that enter the food-groove. Polychaete fan worms, which are also impingement-feeders, are able to hold swimming algae at only one-tenth the efficiency with which they hold inert particles (Dales 1957).

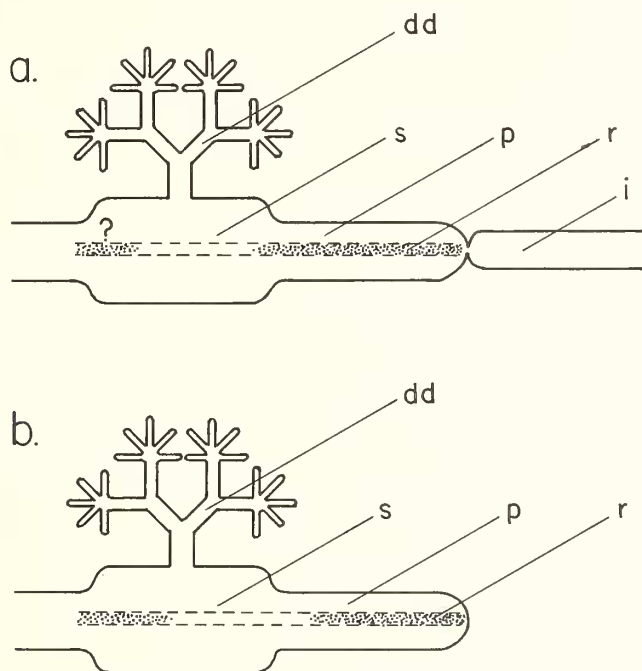
FUNCTIONS OF THE DIGESTIVE ORGANS

Information on the alimentary tracts of brachiopods is available for the inarticulates *Lingula*, *Crania*, and *Discinisca* (Blochmann 1892, 1900; Chuang 1959, 1960), and the articulates *Magellania* (*Waldheimia*) (Joubin 1892), *Pumilus* and *Macandrevia* (Atkins 1958), and *Tegulorhynchia* and *Terebratella* (kindly supplied by G. R. G. Owen). The alimentary tract in both inarticulates and articulates includes pharynx, oesophagus, so-called anterior stomach in the inarticulates or stomach in the articulates (here called stomach for both groups), digestive diverticula, and so-called posterior stomach in the inarticulates or intestine in the articulates (here called pylorus for both groups). The articulate gut is blind and terminates at the end of the pylorus, whereas in the inarticulates it is continuous and has an intestine connected by an anus to the outside (see text-fig. 1A, B). In general the number of digestive diverticula is constant within a species but varies between species (see Blochmann 1892, 1900; Hyman 1959, p. 552; Chuang 1959, 1960); each diverticulum typically consists of bunches of blind acini which are connected to the stomach chamber by a series of branching ducts.

The only detailed description of the functions of a brachiopod gut has been given by Chuang (1959) for *Lingula unguis*. He noted that when this species is feeding, the mucus-bound string containing trapped food particles is carried by ciliary currents through the mouth and into the pharynx in little shreds. He did not indicate how the shredding process takes place. Chuang also described the stomach contents of *L. unguis* as 'fluid and particles'; this description implies that after ingestion, potential food particles are released from their binding mucus in order for digestion to occur. Yonge (1935) studied a number of species belonging to several phyla that transport trapped particles in mucus. He found in all cases that the stomach pH approximates the value at which the mucus in question is least viscous,

and therefore least able to hold its trapped particles. Although no brachiopods were studied by Yonge, it seems reasonable to assume that pH of the lingulid stomach is also responsible for breaking down mucus and releasing food.

The walls of the alimentary tract in both groups of brachiopods are muscular (see Joubin 1892; Blochmann 1892, 1900; Chuang 1959, 1960). Both Joubin (1892) and Chuang (1959, 1960) noted that the guts are lined throughout with columnar epithelium which is ciliated everywhere except for the acini of the digestive diverticula. Ciliary currents in the alimentary tract are generally directed in a posterior direction (Atkins 1958; Chuang 1959), although a strong anteriorly flowing current occurs along the mid-ventral line in the articulate stomach (Atkins 1958).



TEXT-FIG. 1. *a*, schematic diagram of inarticulate gut. Based on information in Chuang (1959). *b*, schematic diagram of articulate gut. Based on information from Atkins in Morton (1960). dd, digestive diverticula; i, intestine; p, pylorus; r, mucus-bound rod; s, stomach.

According to Chuang (1959) the posteriorly directed currents in *Lingula* serve only to keep the gut contents agitated and mixed, and muscular action of the gut walls is responsible for through-going movement of the contents. Also, in both inarticulates and articulates, a clockwise rotation (when viewed from the anterior end) is produced by the beating of cilia in both the anterior region of the stomach and posterior region of the pylorus (Atkins 1958; Chuang 1959; Owen, written communication); rotation is stronger and faster in the pylorus (Chuang 1959; Morton 1960).

When *L. unguis* is actively feeding and digesting, ciliary rotation in the stomach ceases or greatly decreases, and the digestive diverticula undergo muscular pulsations (Chuang 1959). These pulsations appear to occur universally among brachiopods. In *L. unguis* each diverticulum in turn relaxes usually in order of position, anteriorly to posteriorly, causing the branching ducts and acini to expand and suck in fluid and particles from the stomach. No sorting or rejection of the ingested material takes place in the stomach of either group (Chuang 1959; Owen, written communication), and all ingested particles stand a chance of being sucked into the digestive diverticula. Relaxation is followed by a contraction which forces the fluid and particles back into the stomach. Chuang (1959) noted that the number of cycles of relaxation and contraction varied from one to twelve (on the average about four) per minute depending on size of the individual and phase in the feeding cycle; he stated that at the height of feeding activity in one specimen, the pulsation rate was twelve per minute (an unusually fast rate), slowing down to three per minute one and a half hours later when most of the particles had left the stomach; time for relaxation was usually about ten times that for contraction. Owen observed (written communication) that particles visible to him in the acini of *Tegulorhynchia* and *Terebratella* appeared to move toward the stomach during contraction but remained stationary during relaxation; he suggested that relaxation of the acini may have been so slow that only the fluid and particles too fine to be visible under the binocular were drawn into the acini. Judging from Chuang's descriptions of changes in rate of pulsation within a single specimen, it appears that Owen's observations may be typical of a specimen at a particular phase of its feeding activity. Owen also noted that cilia occurring where the ducts of the digestive diverticula meet the stomach all beat into the stomach. Chuang (1959) observed that cilia in the branching ducts beat toward the stomach and are responsible for a strong outer current along the walls and a weaker current going toward the acini in the middle of the ducts. Particles in the ducts get passed from one ciliary current to the other, suggesting to Chuang that the function of the currents is to keep the contents of the digestive diverticula mixed.

According to Chuang (1959) most intracellular digestion in brachiopods appears to occur in the acini of the digestive diverticula. These acini in *L. unguis* are tubular to globular sacs (Chuang 1959) and in *Tegulorhynchia* and *Terebratella* are long, finger-like and unbranched (Owen, written communication). Both Joubin (1892) and Chuang (1959, 1960) noted that, unlike the epithelial lining of the rest of the digestive tract, that of the acini is unciliated. Blochmann (1892), however, reported that ciliated epithelium lines the digestive diverticula of *Crania anomala*. However, Blochmann found it difficult to section the digestive diverticula, and erroneously thought that the epithelial structure in both acini and ducts is the same, but differs from that in the rest of the gut. One therefore suspects that Blochmann was actually describing epithelium of the ducts rather than that of the acini of the digestive diverticula. Chuang (1959, 1960) has shown that in both *Lingula* and *Crania* the cells lining the acini, unlike those of the rest of the gut, bulge into the lumen at various heights and form an uneven surface. Two kinds of cells occur in the digestive diverticula of brachiopods, as noted by Joubin (1892) in *Magellania* and by Owen (written communication) in *Tegulorhynchia* and *Terebratella*.

Yonge (1926*a, b*) showed that bulges on the diverticular cells of filter-feeding bivalves are pseudopodial extensions which phagocytose fine particles of solid matter and absorb soluble material; more recent evidence shows that these digestive cells also take in particulate matter by pinocytosis (Owen 1970). The same is true in brachiopods. Professor Owen reports on *Tegulorhynchia* and *Terebratella*: 'I have clear evidence of the ability of the large digestive cells to ingest particulate material both by phagocytosis and pinocytosis and it is clear from a preliminary examination under the microscope that these digestive cells, as in bivalves, possess a well-developed lysosomal system which serves to process the ingested material.'

Apart from the digestive cells, epithelial cells of another type, basiphil cells, also occur in diverticular tubules of all bivalves (Sumner 1966; McQuiston 1969; Owen 1970, 1974; Pal 1971). In filter-feeding bivalves basiphil cells are present in the crypts of these tubules; the basiphil cells may be flagellated, or if not flagellated, another type of flagellated cell may be associated with them (Owen 1974). Similar cells were noted by Professor Owen in the digestive diverticula of the articulate brachiopods *Tegulorhynchia* and *Terebratella*; he writes: 'The tubules [i.e. acini] possess flagella and it is almost certain that, as in bivalves, these are borne by the dark staining cells of the crypts.' Although Joubin's (1892) descriptions of the two types of cells that occur in the digestive diverticula of *Magellania* are not very detailed in comparison to the much more recent descriptions for bivalves, his Type 2 cells 'qui contiennent toutes, vers leur tiers supérieur, un amas de grosses granulations', probably correspond to vacuolated (digestive) cells found in bivalves, and his Type 3 cells, which differ from Type 2 'par le diametre plus petit des granulations . . . répandu[e]s dans toute l'étendue de la cellule', may correspond to the basiphil cells of bivalves with their finely granular cytoplasm but no vacuoles (cf. Sumner 1966). Recent evidence suggests that the basiphil cell in bivalves is secretory (Sumner 1966; McQuiston 1969; Owen 1970), although this interpretation has been disputed by Pal (1971). There is no information on the function of basiphil-like cells in brachiopods, but it probably corresponds to that of basiphil cells in bivalves.

Chuang (1959, 1960) noted that epithelial bulges in the inarticulate acini break away and form blobs of various sizes in the lumen of the digestive diverticula. Similar discharge that occurs in filter-feeding bivalves is now attributed to cyclic disintegration of their absorptive cells following completion of intracellular digestion (Purchon 1971; Morton 1973). There are no data on possible cyclicity in brachiopods. Indigestible particles that brachiopods take into the cells of the digestive diverticula are probably expelled in these blobs, as Owen (1955) described for bivalves.

Brachiopods all appear to have a ciliated epithelial groove which begins in the stomach chamber and extends to the posterior end of the pylorus (Joubin 1892; Blochmann 1900; Atkins 1958; Chuang 1959, 1960). In *Lingula*, the only genus for which there is detailed information, the epithelial groove arises in the vicinity of the digestive diverticulum that is situated most posteriorly; according to Blochmann (1900) it begins just behind the entrance to the posterior digestive diverticulum in *L. anatina*; whereas Chuang (1959) noted that in *L. unguis* it starts in the anterior ducts of this same posterior diverticulum. In *Lingula*, particles that are rejected by the digestive diverticula are bound into a mucous rope in the ciliated epithelial groove and transported within it by ciliary currents to the pylorus (Chuang 1959). The

rejected material, similar to that in the intestinal groove of bivalves, is isolated from the region of active feeding in the stomach, and therefore should not contaminate those particles that are being actively passed back and forth between the stomach and digestive diverticula. Chuang (1959) reported that in *L. unguis* the mucus-bound rope may leave the groove at the posterior end of the pylorus and rotate axially in a manner somewhat reminiscent of the crystalline style of bivalves. Atkins (1958) noted that in the articulate the rotating string of mucus-bound particles that is found in the pylorus may stretch into the stomach and come under the influence of the anterior rotating region, thus being rotated at both ends. Atkins called the rotating string a protostyle. However, as in *Lingula*, ciliary rotation probably ceases in the articulate stomach during muscular pulsations of the digestive diverticula. Thus it is probable that growth of the rotating string anteriorly into the stomach only occurs after active digestion has ceased. But rotating mucus-bound matter in the anterior rotating region need not be only the result of growth of the protostyle anteriorly; both Atkins (1958) and Morton (1960) suggested that after digestion is complete in the articulates, unused material is expelled from the digestive diverticula into the stomach where it is bound by mucus and rolled into a bolus by the anterior rotating area; and products of disintegration of the digestive diverticula might periodically be discharged *en masse* into the stomach, if feeding processes in brachiopods are cyclic.

The processes that take place in the brachiopod stomach include both the disintegration of mucus and the formation of a mucus-bound anterior cord. Goblet-shaped mucus cells generally occur among epithelial cells of the digestive tract (Joubin 1892; Blochmann 1892, 1900; Chuang 1959, 1960). However, stomach conditions that favoured the breakdown of mucus that bound the incoming food particles would not favour the formation of a faecal cord that is bound by the same kind of mucus. If the incoming mucus breaks down chemically because of the pH of the stomach, either there must be a change in the stomach pH after digestion, or mucus that is produced in the stomach must differ from that formed in the food-groove, and have its lowest viscosity at a different pH. Stomach pH in bivalves decreases when the digestive diverticula break down and discharge their relatively acidic products into the stomach (Purchon 1971; Morton 1973); the same may occur in brachiopods.

There is no record of an anterior mucus-bound string being formed in the rotating area of the inarticulate stomach. However, it seems likely that at the end of the muscular contractions of the digestive diverticula, undigested material would be expelled into the stomach, as has been postulated for the articulates; large numbers of globules from the digestive diverticula might also be shed into the stomach; but whether this material is then passed into the pylorus bound in mucus, or unbound, is unknown. If it is passed unbound, the inarticulates would not require changes in stomach conditions that would permit breakdown of mucus at one time and its formation at another. If mucus disintegrates in one part of the inarticulate gut and is produced in another part, it is possible that pH differs in different parts of the gut. Such is the case in some other invertebrates (Yonge 1935). The only information on pH of the inarticulate gut indicates that it is the same throughout (Chuang 1959). However, it is possible that a difference in pH is present only at certain times during

the feeding process, and that none of the animals tested by Chuang were at the critical feeding stage.

In the articulates the part of the gut where posterior rotation occurs is usually referred to as the 'intestine', and according to Atkins (1958), it may be considered embryologically and functionally to be intestine. In the inarticulates this rotating region is called 'posterior stomach' by Chuang (1959, 1960). The area is morphologically, physiologically, and histologically similar in both groups of brachiopods, and, according to Morton (1960), similar in function to the pylorus of other impingement-feeders. Thus it seems best to call the posterior rotating area of all brachiopods the 'pyloris' (as Morton appeared inclined to do), instead of using different names for each group. The brachiopod pylorus also resembles the style sac of molluscs (Atkins 1958; Chuang 1959).

In the inarticulate gut a sphincter occurs at the posterior end of the pylorus, and by relaxing at regular intervals it enables waste material to empty by peristalsis into the intestine (Chuang 1959). An anal sphincter is also present; its relaxation permits intestinal contents to be expelled, also by peristalsis. Because of the blind gut in the articulates, their faecal matter is expelled through the mouth by antiperistalsis (Richards 1952; Atkins 1958); their stomach cord must be eliminated with each defecation, while that in the pylorus is possibly expelled only occasionally. Rejected material is packed into pellets by the intestine in the inarticulates, and, according to Morton (1960), probably at the oesophageal end of the stomach in the articulates. In both cases pellets are expelled into the mantle cavity. Rudwick (1962) described for the articulates how a faecal pellet, after it leaves the mouth, is transported by the filaments and by the cilia of the mantle surface to the postero-lateral corner of the shell, whence it is expelled by rapid closure of the valves. Likewise, inarticulates eject pellets by sudden snapping of the valves (Rudwick 1970, p. 123), probably also each time one is produced, for if faecal matter is not immediately expelled from the valves, fouling of the mantle cavity is possible even though the pellets are bound in mucus.

Both types of brachiopods are functionally suited for ingestion and digestion of particulate material, and expulsion of particulate wastes. The articulate gut is not reduced so that its prime food must be dissolved and colloidal material as suggested by McCammon (1969), nor, as is apparent from a later discussion of enzymes, is the pylorus reduced to being able to absorb nothing at all, as suggested by McCammon and Reynolds (1972).

The only gross difference between the alimentary tracts of the two groups of brachiopods is that in the articulates the gut is blind and ends with the pylorus, and in the inarticulates it is through-going and ends in an anus. In other respects the digestive tracts are morphologically and histologically similar. Although information on digestive processes in brachiopods is relatively detailed only for *L. unguis*, evidence for other species, when present, always either corroborates or complements that from *L. unguis* (except when concerning expulsion). It is therefore suggested that, except in the expulsion of waste, very similar physiological processes occur in the alimentary tracts of both kinds of brachiopods.

RELATIVE FEEDING EFFICIENCIES OF THE INARTICULATES
AND ARTICULATES

The feeding process in the articulates has not been considered as efficient as that in the inarticulates, because with each defecation an articulate must cease feeding and expel its stomach contents. However, there is evidence to suggest that the articulate method of expelling faeces through the mouth has little disadvantage over the inarticulate method of expulsion through the anus. Ingestion should cease as soon as the brachiopod stomach is full, and it should not resume until after digestion has occurred and the stomach has emptied. Therefore intake of food particles should have ceased in articulates some time before expulsion of wastes through the mouth. But even if food intake is continuous, ingestion must cease when the valves close, and both kinds of brachiopods rid the mantle cavity of faecal pellets by sudden snapping of the valves; therefore, the articulates are unlikely to have a disadvantage unless they spend appreciably more time in expelling wastes than the inarticulates. The only information available on rate of expulsion indicates that the articulates eliminate only one or two faecal pellets per hour and close their valves for just a few minutes each time (see Savage 1972). Since the articulates appear to spend only a small percentage of their time expelling wastes, they are unlikely to lose significantly more potential feeding time than the inarticulates because of this function. Digestion in both groups of animals probably ceases during defecation; it is obvious that it must in the articulates; and although it is not so obvious in the inarticulates, Chuang (1959) noted that the pulsation rate of the digestive diverticula in *Lingula* is substantially reduced when gut contents pass from the pylorus into the intestine. The relative efficiencies of inarticulates and articulates appear to be comparable.

BRACHIOPOD FOOD

Few controlled experiments have been done in order to determine what brachiopods can ingest and digest. No field studies appear to have shown what they live on under natural conditions, and, as Cowen (1971) has indicated, the food of any particular specimen probably depends on habitat, latitude, depth, and season. As described above, it appears that all brachiopods trap, ingest, and digest food material in a similar manner, and thus all brachiopods are grouped in this section.

Ingestion. Most information on particulate material ingested by brachiopods is from the contents of their alimentary tracts. However, not all material that is trapped may be present in the gut at the time of dissection, for easily digestible material may have been assimilated without leaving a trace. Also small forms, such as bacteria, easily escape detection under a microscope.

The particulate material in brachiopod guts appears to consist primarily of micro-organisms and inert particles in varying proportions. Large percentages of clay particles have been reported from the guts of numerous specimens (McCammon 1969; Levinton and Suchanek 1972; Suchanek and Levinton 1974). Diatoms and dinoflagellates are the micro-organisms most frequently found (Blochmann 1900; Rudwick 1965, p. H205; McCammon 1969; Levinton and Suchanek 1972; Suchanek and Levinton 1974). If, as discussed above, large motile protists readily escape

from brachiopod filaments, non-swimming micro-organisms should be ingested more frequently than swimming forms. However, there is no information on the relative sizes and numbers of swimming and non-swimming forms that have been found in brachiopods. Levinton and Suchanek (1972) gave the names of several diatom genera abundantly found in the guts of the brachiopods they dissected, and all are non-motile. This favours the theory of easy escape of swimming forms, although the genera mentioned by these authors may not be representative of the entire contents of the guts of the specimens they dissected or of brachiopods in general. Blochmann (1900) reported the presence of tests of motile forms such as armoured dinoflagellates, small foraminifera, and bivalve and gastropod larvae; his descriptions imply that the tests were empty, and if that were the case, they were probably empty when ingested (for reasons given later). Owen (written communication) noted that in the stomach contents of the specimens of *Terebratella* he studied, apart from diatoms, there were sponge spicules and sand grains (the latter of rather constant size); and that the compact rod in the pylorus appeared to consist largely of these sand grains embedded in mucus.

Digestion. It is necessary to differentiate here between ingestible and digestible material. Most evidence presented on the particulate food of brachiopods has been based on gut contents. But because all material that is trapped by the lophophore is indiscriminately passed to the mouth and into the gut, both digestible and indigestible material is likely to be taken in in various proportions. Easily digested material may be assimilated relatively quickly so that no trace of it remains at the time of dissection. In view of the similarities with bivalves, it is significant that Ballantine and Morton (1956) found no evidence of minute and naked flagellates in the guts of the bivalve *Lasaea rubra*, only a short time after these protists had been eaten. Reid (written communication) states that naked micro-organisms are unrecognizable minutes after entering an oyster stomach. Also, as noted above, particulate waste material is not continuously expelled by brachiopods, but accumulates in mucus-bound cords and is retained temporarily in the stomach and pylorus. Therefore, brachiopod gut contents may at times be a better indication of indigestible than of digestible material. In fact McCammon (1969) noted that the material she recovered from brachiopod guts was in most cases compacted into a bolus. Levinton and Suchanek (1972) reported the heavy-walled diatom *Thalassiosira* occurring commonly in gut contents of shallow-water *Terebratalia*; Ballantine and Morton (1956) showed that the bivalve *L. rubra* could only slightly digest this diatom genus, and that most of the cells were passed out in faeces. The degree of assimilation of much material varies with its retention time in the stomach; if a relatively large percentage of ingested matter is easily assimilated, the rate of renewal of stomach contents might be too fast for the more resistant forms to be decomposed; a longer retention time might permit at least partial breakdown of these forms.

In spite of the above limitations some information on brachiopod food can be inferred from gut contents. Prior to McCammon's (1969) study it was assumed that brachiopods feed chiefly on diatoms and dinoflagellates (see Rudwick 1965, p. H205). McCammon noted a large percentage of clay in the guts of the specimens she dissected, and concluded that these animals obtain much of their nourishment from

material that is sorbed on the surface of clay particles. This conclusion seems reasonable since most of her animals were collected from deep water where other food is likely to be scarce. McCammon assumed the sorbed material to be organic colloids, and there is evidence to suggest (Verwey 1952) that colloids are a source of nutrition for bivalves. However, Newell (1965) showed that the deposit-feeding bivalve *Macoma balthica* digests bacteria that coat ingested particles of mud and organic debris. Newell suggested that suspension-feeders with fine-grained sediment in the guts may also feed on bacteria. Since bacterial concentrations may be high in the top centimetre of marine mud (Jørgensen 1966, pp. 216, 286), it is possible that McCammon's brachiopods were utilizing such bacteria as well as, or instead of, organic colloids.

Laboratory experiments have shown that brachiopods can assimilate certain dissolved substances. After placing *Terebratalia transversa* into dilute suspensions of radioactive glucose, McCammon and Reynolds (1972) were able to trace the uptake of C^{14} through the surfaces of the lophophore and mantle, and then trace the subsequent transport of nutrient products to muscles and other tissues. The experiment lends support to McCammon's (1969) suggestion that several species of articulate brachiopods that survived in the laboratory for up to 2 years lived on dissolved nutrients, the only food that was supplied. McCammon (1973) has also suggested on the basis of histological similarities between the lophophores of *T. transversa* and *Magellania venosa* that *M. venosa* is able to absorb dissolved material in the same way. However, uptake of dissolved nutrients, including uptake through the body wall, is common in invertebrates that feed primarily on other things (Stephens 1968; Southward and Southward 1972*a, b*), and it may occur in many brachiopods. But, as these authors and others have stressed, the ability of a species to assimilate dissolved compounds is not an indication that the animal depends heavily on this type of food, but rather that it has the ability to use dissolved material to augment the rest of its diet. Another potential food of brachiopods may be the loosely compacted organic-mineral aggregates found by Rhoads (1973) and Johnson (1974) to occur commonly at the sediment-water interface in shelf deposits. These aggregates consist of an amorphous matrix containing mineral particles that range in size from a few to several hundred microns in diameter. They appear to be faecal material, and should be high in bacteria (Rhoads 1973; Johnson 1974).

To determine the methods used by *Lingula unguis* in assimilating food particles, Chuang (1959) fed starved specimens with carmine particles in one experiment, and with an emulsion of olive oil in a second experiment. The animals were killed one day after feeding began, and microscopic examination of both fixed and fresh specimens revealed globules of ingested material in most regions of the digestive tract: in both epithelial and mesothelial cells throughout the gut, and in wandering phagocytes that were found among the intestinal contents or among the epithelial cells of the stomach, pylorus, and intestine. (Wandering phagocytes (amoebocytes) are found in both groups of brachiopods (Joubin 1892; Chuang 1959, 1960); in *Lingula* they are reported by Chuang (1959) to occur both in the lumen and among epithelial cells of the gut; Joubin (1892) discussed their presence among the epithelial cells in *Magellania*, but did not report them in the lumen of its digestive tract.)

In the epithelial cells of the acini, Chuang (1959) found carmine particles up to

1.2 μm in diameter and oil droplets 0.8–0.9 μm in diameter. Smaller particles of both substances were present in mesothelial cells of the digestive diverticula. The epithelium and mesothelium of the rest of the gut also contained both carmine and oil: carmine particles were about 0.4 μm in diameter in epithelial cells of the stomach and pylorus, and up to 1.2 μm in the intestine; oil droplets were as large as 5 μm throughout. Wandering phagocytes in the lumen of the intestine held carmine particles that reached 2 μm diameter; those in the epithelial cells of the stomach, pylorus, and intestine contained oil droplets as large as 2 μm . Oil droplets were also found in phagocytes that occurred in the intestinal contents. Chuang (1959) observed that olive oil accumulated in *L. unguis* largely in the epithelium of the acini of the digestive diverticula. He concluded that the epithelial cells of the acini are the chief sites of ingestion. Phagocytes may pick up food from the epithelium and carry it throughout the body as Joubin (1892) noted in *M. venosa*, and as Yonge (1926a) similarly noted in the bivalve *Ostrea edulis*. Chuang (1959) observed that wandering phagocytes in the lumen of the gut of *L. unguis* ingested food particles; but he thought that these cells remained too scarce to play an important role in digestion, even though they increased in numbers after an animal had fed. Chuang's experiments showed that particles that had been engulfed by wandering phagocytes were larger than those found in the epithelial cells (oil droplets amalgamated to form larger masses in the mesothelium). On the basis of similar observations in bivalves, Yonge (1926a, b) and Takatsuki (1934) suggested that the role of free phagocytes is to take in particles that are too large to be ingested by the diverticular cells. Joubin (1892) reported to have observed food particles pass unaided between cells of the stomach epithelium of *M. venosa*; it is difficult to imagine a mechanism of transport, unless the particles were carried by phagocytes, as Yonge (1926a) observed in *O. edulis*. However, phagocytic action does not seem to be important in the lumen of the digestive tract of all bivalve species at all times (see George 1952; Ballantine and Morton 1956); the same may be true for brachiopods. Chuang (1959) also suggested that food particles may be ingested by epithelial cells of the gut wall, but since these cells are non-phagocytic it seems improbable that they are able to directly ingest particulate material. Particles found in cells of the gut wall of *L. unguis* can be explained by phagocytic transfer from the lumen through the wall (a possibility not completely rejected by Chuang), or by similar transfer from sites of ingestion in the acini.

It is also necessary to consider the biochemistry of digestion in brachiopods. In digestion, large molecules of food matter undergo hydrolysis in the presence of enzymes (organic catalysts) and are broken down into small molecules. This breakdown may occur intracellularly or extracellularly; if intracellular, the particles are taken into cells by phagocytosis and pinocytosis and there they encounter intracellular enzymes; in extracellular digestion, hydrolysis of food particles is catalysed by enzymes that are in the lumen of the gut (extracellular enzymes), and particles that are too large to be digested intracellularly are reduced in size sufficiently to be phagocytosed or to be absorbed by the gut epithelium. The assimilated material is transferred to other parts of the organism for storage and subsequent uses in metabolic processes. As it is characteristic of enzymes to catalyse one kind of reaction (i.e. reactions involving substrates with identical linkage between the molecules) or

often one particular reaction (Baldwin 1967, p. 6), the enzymes, their relative strengths, and where they occur in the digestive system of an animal, give some indication of what the animal can digest and how digestion takes place.

Little information has been published on brachiopod enzymes and their distribution. Chuang's (1959) determinations for *L. unguis* are the only published account of an attempt to determine several enzymes in the digestive system of a single brachiopod species. There is also not much information on the natural occurrences of substrates on which these enzymes act. The available data (Tables 1 and 2) on enzymes indicate that carbohydrate digestion in *Lingula* is dominant both intracellularly and extracellularly. Reserve carbohydrates of chlorophyll-bearing plants (amylose and sucrose) and the digestive product of starch (maltose) appear to be important foods for *Lingula*; as they appear to be for marine invertebrates in general (see Kristensen 1972). It is not clear why lactase is strong in certain regions of the alimentary tract,

TABLE 1. Enzyme occurrences in the digestive tracts of brachiopods.

		STOMACH	STOMACH CONTENTS	DIGESTIVE DIVERTICULA	PYLORIS	INTESTINE	WHOLE DIGESTIVE TRACT	TOTAL ORGANISM
□ <i>Lingula unguis</i> ◇ <i>Lingula lingula</i> ○ <i>Coptothyris grayi</i> ● very strong ◐ strong ◑ moderate ◒ weak ◓ absent								
PROTEASE		◓ ₁	◓ ₁	◓ ₁	◓ ₁	◓ ₁		◓ ₅
LIPASE		◓ ₁	◓ ₁	◓ ₁	◓ ₁	◓ ₁		
CARBOHYDRASES	AMYLASE	◐ ₁	◐ ₁	◐ ₁	◐ ₁	◐ ₁		
	ALGINASE			◓ ₂				
	LAMINARANASE			◒ ₃				
	SUCRASE			◐ ₁		◐ ₁		
	INULASE			◐ ₁		◓ ₁		
	RAFFINASE			◓ ₁		◓ ₁		
	MALTASE			◐ ₁		◐ ₁		
	LACTASE			◐ ₁		◐ ₁		
	METHYLCELLULOSE			◓ ₄			◑ ₆	
	CHITINASE						◓ ₆	
METHYLCHITINASE						◑ ₆		

1. Chuang (1959).

2. Favorov and Vaskovsky (1971).

3. Sova *et al.* (1970).

4. Yokoe and Yasumasu (1964).

5. Kozlovskaya and Vaskovsky (1970).

6. Elyakova (1972).

TABLE 2. Enzymes that are referred to in the text, their substrates, and known occurrences of substrates.

Enzymes	Substrate hydrolysed by enzyme	Natural occurrences of substrates
Amylase	Amylose (starch)	Reserve material of all chlorophyll-containing plants (1).
Laminaranase	Laminaran	Reserve material that is ubiquitous in brown algae (3). Important reserve in diatoms (3). Also found in Chrysophyta and euglenoids (1). Polysaccharides similar to laminaran probably most common polysaccharides in nature; in higher plants (3). Similar polysaccharides appear to be important component of marine particulate material (1).
Maltase	Maltose	Sugar that is liberated by digestion of starch; does not often occur free in nature (2, p. 42).
Sucrase	Sucrose	Reserve substance of all chlorophyll-containing plants (1). Various amounts in green and red algae, traces in brown algae (3). Free sucrose rare in animals (1).
Raffinase	Raffinose	Common in higher plants; doubtful if occurs in algae; has been reported from bacteria (1).
Lactase	Lactose	In milk of mammals; occasionally in pollen of higher plants (1).
Alginase	Alginic acid	Major constituent of cell walls of brown algae (4). Has been found in bacteria grown under artificial conditions (1).
Inulase	?	?
Cellulase	Cellulose	In cell walls of higher plants and algae, except blue-green algae (4). Found in fungi and certain bacteria; rare in animals except tunicates (1).
Methylcellulase	Methylcellulose	Degraded cellulose, water soluble (1).
Chitinase	Chitin	Structural component of several invertebrate phyla, particularly arthropods, molluscs, annelids; found in fungi and diatoms (1). Found in cell walls of some green algae (4). Found in yeasts (2, p. 90). Chitinase and cellulase may be identical for cellulase also hydrolyses chitin (Baldwin 1967, p. 75).
Methylchitinase	Methylchitin	Degraded chitin?
Protease	Protein	Found in all plants and animals; main constituent of animals (2, p. 87). Small quantities in cell walls of algae (4). As bulk components of algae but percentages vary (5). As large percentage of growing tips of algae (7).
Lipase	Lipid (fat)	Appears to be found in most plants and animals (2) including algae (6) and bacteria (2). Small quantities in cell walls of algae (4). Forms 10% of body weight of mammals; reservoir of potential chemical energy (2, p. 476).

1. Kristensen 1972.

2. White, Handler and Smith 1968.

3. Meeuse 1962.

4. Kreger 1962.

5. Fowden 1962.

6. Benson and Shibuya 1962.

7. Huang and Giese 1958.

for it is improbable that lactose is a source of food for *Lingula*; Kristensen suggested that lactase in the systems of marine invertebrates may generally attack carbohydrates that have the same molecular linkage as lactose. I could find no information on inulase or its substrate. The indication of a weak laminaranase in the digestive diverticula of the articulate *Coptothyris* is interesting in view of the fact that laminaran is an important reserve in diatoms. However, this information on the strength of laminaranase (Sova *et al.* 1970) may be misleading; for although Sova *et al.* reported weak laminaranase activity in most invertebrates they studied, both Stone and Morton (1958) and Kristensen (1972) found the activities to be relatively strong in general. Methylcellulase (and undoubtedly methylchitinase) in invertebrates is poorly understood; although methylcellulose results only from the breakdown of cellulose, there is often no evidence of cellulase in invertebrate guts (see Barrington 1962; Kristensen 1972; Owen 1974); also there is usually no morphological evidence to indicate that invertebrate guts harbour large quantities of bacteria that are capable

of hydrolysing cellulose (Kristensen 1972). There are many kinds of proteins and lipids in both plants and animals, and, as seen from Table 1, there is the possibility that brachiopods are only weakly able to assimilate some of these, and then only intracellularly. In considering these data on the distribution of proteases and lipases in *Lingula*, one should remember that concentration of extracellular enzymes may vary considerably with time in a single specimen if feeding processes are cyclic. One is also reminded of the negative results obtained in early attempts to determine extracellular proteases and lipases in the digestive tracts of bivalves (see Yonge 1923, 1926a); however, more recent techniques of enzyme determination, superior to those used by Yonge, should have been available both to Chuang, and to Kozlovskaya and Vaskovsky. The apparent lack of an extracellular lipase is supported by Chuang's (1959) observation that olive oil experimentally fed to *L. unguis* was digested only intracellularly. Perhaps brachiopods in general are unable, or only weakly able, to digest proteins and fats extracellularly; the information from Table 1, although scanty, suggests that possibility, for although tests on whole-animal tissues are probably inadequate for detecting weak enzymes, such tests should have indicated the presence of strong proteases in the articulate *Coptothyris*, if they had been present. Enzymes do occur in the intestinal epithelium of *L. unguis*, but these same enzymes are also found in other regions of the digestive tract, showing that matter that is digested in the intestine is also digested elsewhere. It is not known if enzymes in the intestine enable the inarticulates to digest a greater percentage of ingested material than the articulates, or if the articulates compensate for lack of intestinal digestion by relatively more complete digestion anteriorly.

The following general conclusions on brachiopod food can be drawn. In view of similar sizes of digestive cells, not only *L. unguis*, but brachiopods in general, probably cannot phagocytose particles more than about 2 μm across. Dissolved substances, colloidal material, and most bacteria are small enough to undergo intracellular digestion. It is known that dissolved material is used; and available enzyme information shows that dissolved carbohydrates can be absorbed through most of the gut epithelium. Indirect evidence from gut contents suggests that bacteria and/or colloids are also utilized. The apparent dominance of carbohydrases, both intracellular and extracellular, suggests that organic detritus may form a large percentage of the particulate material assimilated by brachiopods; organic detritus is high in carbohydrates and low in proteins and lipids (Agatova and Bogdanov 1972), while living material is high in proteins and low in carbohydrates and lipids (Parsons *et al.* 1961; Agatova and Bogdanov 1972); and the loosely compacted organic-mineral aggregates described by Rhoads (1973) and Johnson (1974) have been shown by Johnson (1974) to be largely carbohydrate. The frequent presence in invertebrate guts of methylchitinase in the absence of chitinase, and methylcellulase in the absence of cellulase, suggests that chitin and cellulose can be hydrolysed by bacteria in detritus; if so, methylchitinase in the absence of chitinase is another indication that organic detritus is a source of food for brachiopods. The strengths of extracellular amylase, and intracellular amylase, sucrase, and maltase indicate that algae form an important part of brachiopod food. The types of whole algae that can be digested must depend on structure and composition of their walls, on the presence of the necessary extracellular enzymes to break down these cell walls in the brachiopod

gut, and on the rate of passage of the algae through the brachiopod gut. A weak laminaranase, if real, suggests that diatoms, often abundant in gut contents, are poorly utilized. Weak proteases, present only intracellularly, indicate that animal forms of life are not important foods for brachiopods and that proteins are probably obtained from other sources.

FOOD OF FOSSIL BRACHIOPODS

The trapping system of fossil brachiopods can be consistently interpreted to be functionally the same as in extant forms (Rudwick 1970, p. 145), and it is probable that the basic structure and functioning of the digestive system is essentially the same throughout the phylum. This degree of morphological uniformity is unlikely to be due to convergence, and is probably a reflection of common ancestry; in which case it can be inferred that the digestive system of brachiopods has remained essentially the same since the Lower Palaeozoic. All major categories of food of extant brachiopods (viz. dissolved substances, bacteria, colloids, organic detritus, and algae) were available throughout the Proterozoic. Thus it appears that the food of fossil brachiopods did not differ basically from that of Recent forms.

FUTURE WORK

Additional data on morphology, histology, physiology, and biochemistry would improve our knowledge of the food and feeding processes in brachiopods, in particular similarities and differences remain to be determined, especially between the inarticulates and articulates. Studies of water-flow around the filaments could determine the kinds of particles that are trapped under various conditions; investigations could ascertain the relative ease with which brachiopods hold motile and non-motile protists. There is need for numerous studies of the alimentary tract, for example to determine the conditions under which ingested particles are released from the mucous cord for digestion, and faecal particles are rebound for expulsion; and to determine if feeding is cyclic (as it appears to be in filter-feeding bivalves) and whether the diverticular cells of brachiopods disintegrate periodically and shed their products into the stomach. The role played by phagocytes in digestion should also be examined. Further data on enzymes would be helpful in indicating what brachiopods can digest and where in their alimentary tracts different kinds of digestion occur: it would also be interesting to know where the extracellular enzymes are produced. More information on brachiopod food can be obtained from feeding experiments performed under controlled conditions. Further studies of uptake of dissolved material and transportation of nutrient products (McCammon and Reynolds 1972) are needed. To acquire direct evidence of what brachiopods are able to digest and the relative efficiencies of digestion of different substances, experiments could be performed similar to some of those of Ballantine and Morton (1956) on the bivalve *Lasaea rubra*. In these studies starved specimens should be fed different species of living micro-organisms, and the amount that is ingested then determined; at certain time intervals after feeding is started, contents from different parts of the gut and from faecal pellets should be examined to see how far digestion

has proceeded in different areas. To determine if brachiopods consume bacteria that are on the surface of mud particles, experiments like Newell's (1965) are needed, where C/N ratios in bacteria-coated mud are determined before and after it passes through the gut. However, all these studies would only set constraints on the range of foods that can be utilized by brachiopods, but without such constraints we cannot judge from gut contents of recently collected animals, or from potential food in the environment, what brachiopods actually live on.

CONCLUSIONS

1. Methods of trapping food particles are nearly identical in all brachiopods.
2. Both inarticulates and articulates ingest and digest particulate material and expel particulate wastes.
3. Except in the expulsion of waste, nearly identical physiological processes appear to occur in the alimentary tracts of both kinds of brachiopods.
4. The articulate method of expelling waste through the mouth appears to have little disadvantage over the inarticulate method of expulsion through the anus.
5. The food of the two kinds of brachiopods is probably essentially the same.
6. Brachiopods are able to assimilate dissolved substances. Indirect evidence suggests that bacteria and colloids are also utilized; that organic detritus in general and some algae are important food sources; and that animal forms of life are not important foods for brachiopods.
7. There is no reason to suggest that the food of fossil brachiopods differed basically from that of extant forms.

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H. MIRIAM STEELE-PETROVIĆ

Department of Geological Sciences
Northwestern University
Evanston, Illinois, 60201
U.S.A.

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